# 盐分、温度及其互作对羊草种子发芽率和幼苗生长的影响

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**摘要:**羊草是多年生优质牧草,也是中国松嫩平原的优势建群植物。研究了羊草种子在 8 种浓度(0、50、100、150、200、300、400 和 500 mmol/L) NaCl 胁迫及将胁迫解除后在 3 种变温(16/28℃、5/28℃ 和 5/35℃)条件下的发芽率以及幼苗的生长变化。双因素方差分析表明,NaCl 胁迫解除前后盐浓度、温度及其互作均极显著影响羊草种子萌发和幼苗生长。胁迫解除前,在 3 种温度下,羊草种子发芽率最高出现在没有盐胁迫的条件下,随着 NaCl 浓度的增加,发芽率呈下降趋势。5/28℃下,NaCl 溶液对种子萌发抑制最小,浓度达到 200 mmol/L 时,仍有 25.3% 的种子萌发;在 5/35℃下,对种子萌发抑制作用最大,浓度超过 100 mmol/L 时,种子萌发被完全抑制;16/28℃的处理介于二者之间。胁迫解除后,羊草种子在 3 种温度下发芽趋势不同。16/28℃下表现为 NaCl 浓度较大的处理发芽率较高,5/28℃下则呈先上升(0 ~ 150 mmol/L)后基本保持不变趋势;5/35℃下则呈先上升后下降趋势。盐胁迫下,羊草幼苗在 16/28℃变温下生长最好,其次为 5/28℃,5/35℃生长最差。盐胁迫解除后,16/28℃和 5/28℃下,0 ~ 100 mmol/L NaCl 处理的幼苗根长和苗长随浓度增加而显著上升,大于此浓度变化较小;在 5/35℃下,100 mmol/L NaCl 处理的幼苗根长和苗长最大,而浓度大于 100mmol/L 时,则随着 NaCl 浓度增加呈下降趋势。

**关键词:**羊草; NaCl; 温度; 发芽率; 幼苗

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# Effects of salinity, temperature and their interaction on the germination percentage and seedling growth of *Leymus chinensis* (Trin.) Tzvel. (Poaceae)

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**Abstract:** *Leymus chinensis* (Trin.) Tzvel. (Poaceae) is a perennial, high quality grass and is the dominant species in Songnen plain, China. Seed germination and seedling growth of *Leymus chinensis* were investigated under eight levels of salinity stress (0, 50, 100, 150, 200, 300, 400, 500 mmol/L NaCl) and three temperature regimes (16/28℃, 5/28℃, and 5/35℃) and then after the salinity stress was removed. The results of a two-way ANOVA showed that salinity (including when the salinity stress was removed), temperature and their interaction significantly affected the seed

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germination and seedling growth of *L. chinensis*. The highest germination percentage was obtained under non-saline conditions, and with an increase of NaCl concentration, germination significantly decreased. Seed germination at the moderate temperature regime of 5/28℃ was optimal, with 25.3% of seeds germinating in 200 mmol/L NaCl. The salinity inhibition for seed germination was greatest at 5/35℃ when no seeds germinated above a concentration of 100 mmol/L NaCl while the salinity inhibition was lightest at 5/28℃. After 18 days, seeds were transferred from salt solutions to distilled water and those from high salinities ( ≥150 mmol/L), the seed germination recovered most quickly at 5/28℃, and slowest at 5/35℃. At 16/28℃, germination percentage increased with the pre-treatment NaCl concentration. At 5/28℃, germination increased between 0 to 150 mmol/L and then changed little when NaCl was more than 150 mmol/L. However, seed germination percentage increased from 0 to 100 mmol/L and then decreased from 100 to 500 mmol/L. Seedling growth was also significantly inhibited by salinities. Under NaCl stress, seedlings grew best at 16/28℃, moderately well at 5/28℃ and seedling growth was significantly inhibited at 5/35℃. Seedlings which germinated after being transferred to distilled water showed different growth patterns with different pre-treatment salinity and temperature regimes. At 16/28℃ and 5/28℃, root and shoot length increased with a pre-treatment NaCl concentration of 0 − 100 mmol/L but changed little when it was more than 100 mmol/L. At 5/35℃, the maximum values of shoot and root length occurred at 100 mmol/L NaCl, and then decreased when the concentration was over 100 mmol/L.

**Key Words**: *Leymus chinensis*; NaCl; temperature; germination percentage; seedling

羊草(*Leymus chinensis*)是赖草属多年生优质牧草,主要分布在欧亚大陆的西伯利亚草原地带,包括俄罗斯外贝加尔湖地区,蒙古共和国的北部和东部部分地区,中国的东北平原、华北平原和内蒙古高原区[1]。羊草具有耐旱、耐寒、耐盐碱、营养价值高和适口性好的特点,是非盐生植物中耐盐碱性最强的物种之一,具有广泛的生态适应性。目前,我国羊草草地退化较为严重,约有90%以上的羊草草地发生了不同程度的退化以及盐碱化[2]。羊草种子由于休眠期长、休眠程度深,已经成为羊草植被恢复的瓶颈问题之一[3,4]。

土壤盐渍化是影响世界农业生产最主要的非生物胁迫之一[5,6]。盐分对种子发芽率、幼根和幼芽的长度,干鲜重等都有一定的影响[7,8],如高盐胁迫能够完全抑制种子的萌发,而低水平条件诱导种子的休眠[8~10]。一般来说,盐生草种子发芽率最高出现在没有盐胁迫的条件下,而随着盐浓度的增加而降低。但不同物种耐盐性存在很大差异,大多数牧草种子在250 ~ 350 mmol/L NaCl中就会显著被抑制[11],而*Spartina alterniflora*在1027 mmol/L NaCl中发芽率也能达到8%[12],*Haloxylon ammodendron*种子在1400 mmol/L NaCl中仍有少数萌发[13]。温度在决定种子萌发中起双重作用,即直接影响种子的萌发或通过间接调节种子休眠影响萌发[14~16]。Baskin和Baskin[17]认为,打破休眠的种子首先在高温下发芽;随着休眠程度的减轻,需要的最低温度下降,从而达到萌发的最大温度范围,即最大程度上解除了休眠。变温能够促进多种植物种子的萌发,而恒温则不利于其萌发[16,18]。羊草种子萌发也具有相似的规律[4]。在25 ~26℃的恒温下以脱脂棉和纱布为发芽床时,羊草种子发芽率仅为1.8%[2]。而10/20℃和10/25℃的变温条件下,羊草种子发芽率分别为37.8%和43.3%,均高于恒温处理[19]。可见,与恒温相比,变温可以刺激羊草种子萌发,显著提高发芽率。

种子萌发和幼苗生长阶段是一个植物种群能否在盐渍环境下定植的关键时期[20,21],盐-温互作在田间条件下对萌发时间具有重要的生态指示性[22]。因此,研究不同温度、盐分及其互作对种子萌发和幼苗生长的影响具有重要的生物学和生态学意义。目前,有关羊草幼苗在盐胁迫下生理响应方面的研究较多[23,24],但对羊草种子萌发期耐盐性研究较少,尤其是盐分与温度互作对羊草种子萌发和幼苗生长的研究还未见报道。东北松嫩平原典型的盐碱化土壤有害盐分主要以$Na^+$、$HCO_3^-$、$CO_3^{2-}$、$Cl^-$为主,含量分别为1541.5、5014.2、432.0和727.8 mg/kg[25],对$Na_2CO_3$对羊草种子萌发进行了研究,研究了NaCl、温度及其互作对羊草种子发芽率和幼苗生长的影响,旨在明确羊草种子萌发和幼苗生长在不同温度下耐盐阈值,从而为羊草植被恢复技术的研发提供理论参考。

## 1 材料与方法

### 1.1 供试材料

供试羊草种子(千粒重约为 2.5g)于 2004 年 7 月末采自中国大安碱地生态试验站(N45°36′, E123°53′)[26]的羊草自然分布群落。采集后的种子在室温下晾干,装入透气布袋中,放在 4℃冰箱内保存、备用。实验前先用 0.1% $HgCl_2$溶液对种子进行表面消毒 10 min,再用蒸馏水冲洗若干次后播种。

### 1.2 实验方法

萌发实验进行时间为 2006 年 7 ~ 8 月。将 NaCl 配成浓度为 0、50、100、150、200、300、400mmol/L 和 500 mmol/L 的溶液。将上述消毒种子放在铺有单层滤纸的 9 cm 玻璃培养皿内,每种处理 3 次重复,每个重复 50 粒羊草种子。每个培养皿内加入 10 ml 上述盐溶液,对照中加 10 ml 蒸馏水,用封口膜封口,以防止溶液蒸发。发芽温度为 16/28℃、5/35℃和 5/28℃,低温 12 h(黑暗),高温 12h(光照,光强 54 $\mu mol \cdot m^{-2} \cdot s^{-1}$)。播种 18 d 之后,测量萌发种子的根长和苗长,计算根/冠比(根长/苗长比)。将未萌发的羊草种子取出,放在铺有新的滤纸培养皿内,用 10 ml 蒸馏水浸泡 24 h 后吸出多余蒸馏水,再统一添加 10 ml 蒸馏水,然后在原来的温度条件下继续萌发。实验结束时计算发芽恢复率(新萌发的种子数/转移到非胁迫条件下的未萌发种子总数 × 100%),记录根长和苗长,计算根/冠比。

## 2 结果与分析

### 2.1 盐分和温度对羊草种子发芽率和幼苗生长的影响

#### 2.1.1 盐分和温度对羊草种子发芽率的影响

从图 1 和图 2 可以看出,3 种变温条件下羊草种子的发芽率均随 NaCl 浓度的升高而下降;相同浓度 NaCl 处理的种子发芽率均在 5/28℃最高,其次是 16/28℃,最低为 5/35℃。在 16/28℃下,对照发芽率为 63.2%,50 mmol/L 浓度处理为 52.2%,其它浓度下发芽率均低于 50%,而当浓度为 300 mmol/L 时,发芽率仅为 1.5%,超过 400 mmol/L 时没有羊草种子萌发。5/28℃条件下,对照的发芽率达到 91.3%,50 ~ 100 mmol/L NaCl 处理的发芽率达到 70% ~80%;而当浓度超过 300 mmol/L 时,发芽率与 16/28℃处理的结果相似。在 5/35℃条件下,对照发芽率为 61.3%,NaCl 浓度为 50 ~ 500 mmol/L 时,发芽率均低于 25.0%,且当浓度超过 150mmol/L 时,发芽率均为 0。双因素方差分析的结果表明,温度、盐度以及二者互作显著影响羊草种子的发芽率(表 1)。

#### 2.1.2 盐分和温度对幼苗生长的影响

从图 3 可以看出,3 种不同温度下,羊草幼苗的根长和苗长均随 NaCl 浓度的增加而降低;相同 NaCl 浓度下表现为 16/28℃ > 5/28℃ > 5/35℃,表明盐分、温度以及二者互作对羊草幼苗的生长也存在一定的影响。NaCl 浓度≤150 mmol/L 时,3 种温度下根/冠比的变化均不明显,而≥200 mmol/L 时(5/35℃除外)呈上升趋势,说明低浓度 NaCl 对羊草的根长和苗长的抑制程度相当,高浓度 NaCl 对苗长的抑制更明显。方差分析结果表明,温度、盐度及其互作对羊草根长和苗长的影响也均达到极显著水平(表 1)。

**表 1 盐分、温度及其互作对羊草种子发芽率和幼苗生长的影响**

**Table 1 Effects of salinity, temperature and their interaction on the germination percentage and seedling growth of *L. chinensis***

| 变异来源 Source of variation | 发芽率 Germination percentage | 根长 Root length | 苗长 Shoot length |
|---|---|---|---|
| 盐分 Salinity | 256.1 | 319.6 | 262.6 |
| 温度 Temperature | 178.9 | 20.7 | 402.5 |
| 盐分×温度 Salinity × Temperature | 48.8 | 272.1 | 36.9 |

表中数据为双因素分析的 $F$ 值,显著水平均为 $P<0.001$; Data are $F$ values (Two-way ANOVA) significant at $p<0.001$

### 2.2 盐胁迫解除后羊草种子发芽率和幼苗生长

#### 2.2.1 盐胁迫解除后对羊草种子发芽率影响

盐胁迫解除后,羊草种子的发芽率在不同变温条件下也存在较大的差异(图 4)。双因素方差分析结果表

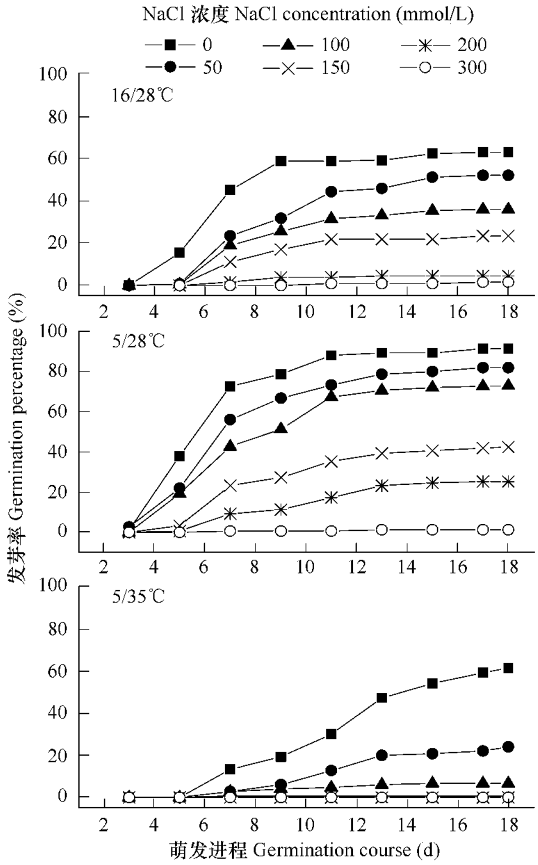


图 1　盐分和温度对羊草种子萌发进程的影响

Fig. 1　Effects of salinity and temperature on the germination course of *L. chinensis*

当 NaCl 浓度超过 400 mmol/L 时羊草种子发芽率均为 0,没有在图中表示　When the NaCl concentration≤400 mmol/L, no germinated seed was observed and therefore the data was not showed in the figure

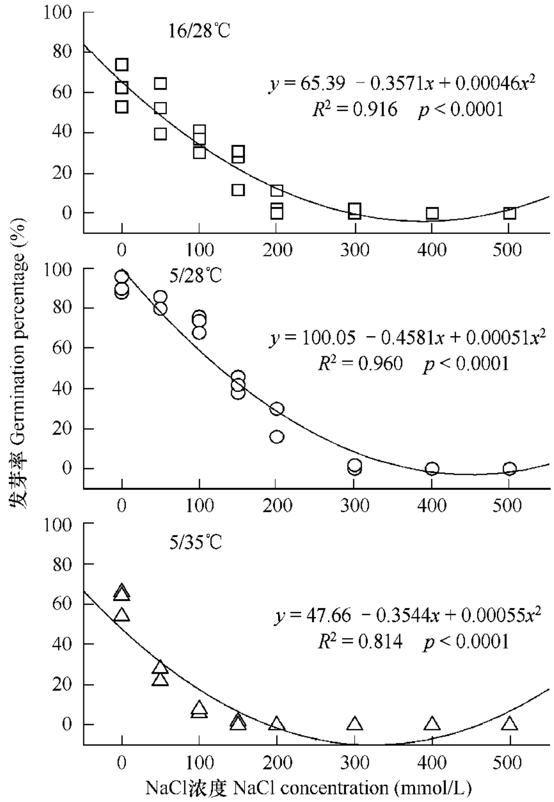


图 2　3 种温度下羊草种子发芽率与 NaCl 浓度的关系

Fig. 2　Relationship between the seed germination percentage of *L. chinensis* and NaCl concentration under three temperature regimes

明,温度和原盐浓度对羊草种子的发芽率具有极显著的影响(表 2)。在 16/28℃条件下,随着原 NaCl 浓度的增加,羊草种子发芽率呈显著上升趋势;原浓度 500 mmol/L NaCl 时的发芽率最高,达到 55.3%,与对照相比提高了 45.9%($p$<0.05)。在 5/28℃条件下,0 ~ 150 mmol/L NaCl 范围内,随原盐浓度的增加,发芽率呈显著上升趋势,原 150 mmol/L NaCl 处理下的种子达到最大值为 71.5%,而在 150 ~ 500 mmol/L 下处理的羊草种子发芽率在 58.0 ~ 65.3%之间,经多重比较,没有显著差异。在 5/35℃条件下,羊草种子发芽率随着原胁迫盐浓度的上升呈现先上升后下降的趋势,50 mmol/L 时最高为 49.1%,分别比对照和 500 mmol/L 处理高 18.1%和 40.1%。

### 2.2.2　盐胁迫解除后对羊草幼苗生长的影响

从图 5 和表 2 可以看出,原盐浓度、温度及其互作对羊草根长和苗长均存在显著影响。在 16/28℃和 5/28℃下,根长和苗长随着 NaCl 浓度的升高均表现为先上升,后保持相对稳定的趋势。原 NaCl 浓度在 0 ~ 50 mmol/L 时,16/28℃下羊草幼苗的根长和苗长均低于 5/28℃,100 ~ 500 mmol/L 时则均高于 5/28℃的处理。5/35℃条件下,随着原胁迫 NaCl 浓度的升高均表现为先上升后下降趋势,100 mmol/L 时,羊草幼苗的根长(1.7 cm)和苗长(3.0 cm)最大,分别为对照的 130.8%和 136.4%;500 mmol/L 处理分别为对照的 15.4%和 36.4%。3 种温度下根/冠比则基本上表现为下降趋势。双因素方差分析结果表明,温度、盐胁迫解除前的浓度以及二者互作也显著影响羊草种子的根长和苗长(表 2)。

## 3 讨论

盐胁迫对植物种子萌发有以下几种可能:(1)阻止种子萌发,但不使种子丧失活力;(2)延迟但不阻止种子萌发[18];(3)当盐浓度高到一定程度或持续一定时间还有可能造成种子永久性失去活力[27]。不同的盐生植物在萌发时期的耐盐性不同[28],本实验中,羊草种子的发芽率随 NaCl 浓度的增加而下降;当解除胁迫后,随着 NaCl 浓度的增加,羊草种子发芽率出现增加趋势,表明一定浓度下,盐分延迟了种子萌发,但大部分种子没有失去活力。NaCl 对发芽抑制作用可能是以下原因造成的:增加了溶液的渗透势,从而抑制羊草种子萌发;离子毒害可能会造成少数种子的永久性失活;盐分造成了部分羊草种子强迫性休眠,因为盐胁迫解除后,在适宜的温度条件下仍然有较高的发芽率;盐分对胚的直接影响造成的。本文结果表明,当 NaCl 浓度超过 50 mmol/L 时就显著抑制了羊草种子的发芽率,这与周婵等[29]的 50 ~600 mmol/L NaCl 对羊草种子的萌发均有促进作用的结论不同。本实验认为,如果 NaCl 对羊草种子的发芽率具有促进作用,这一阈值应当在低于 50 mmol/L 的范围内。NaCl 抑制羊草种子萌发的具体原因以及阈值还需要进一步深入研究。

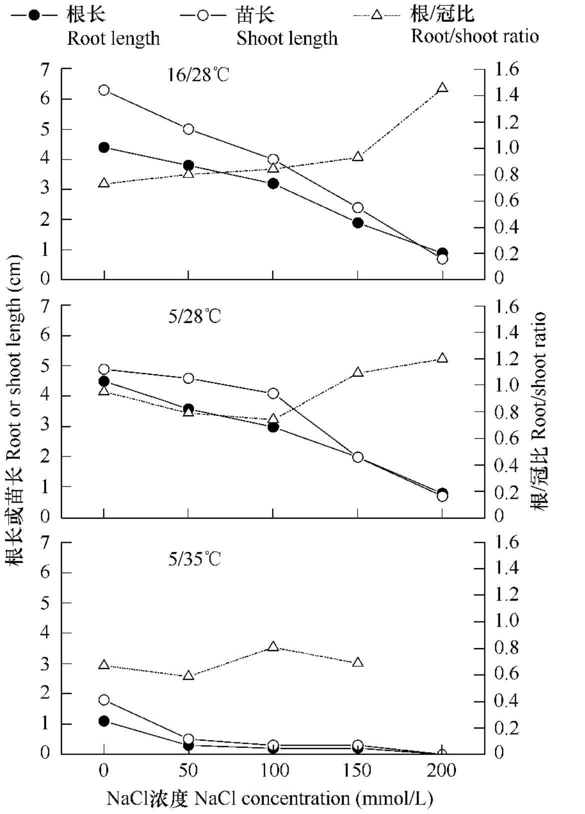


图3 盐分和温度对羊草幼苗生长的影响

Fig. 3 Effects of salinity and temperature regime on seedling growth of *L. chinensis*

当浓度超过 200 mmol/L 根长和苗长图中没有表示. Data was not shown in the figure when the NaCl concentration exceeded 200 mmol/L

温度是决定种子萌发的主要条件之一,对种子的休眠、休眠的减轻或加深至幼苗的形成整个过程均起着重要的作用[30]。本文研究表明,温度显著影响羊草种子的发芽率,是羊草种子休眠和萌发的最关键因素之一。5/28℃下羊草种子发芽率显著高于 5/35℃和 16/28℃。温度对种子休眠和萌发的影响,可能原因包括温度影响种子的膜透性、膜结合蛋白的活力、水解酶的活性以及种子内物质的代谢[31]、促进赤霉素 $GA_3$、细胞分裂素和 ABA 合成,降解或转化[32]等,但在羊草中还缺乏有关机理的研究。

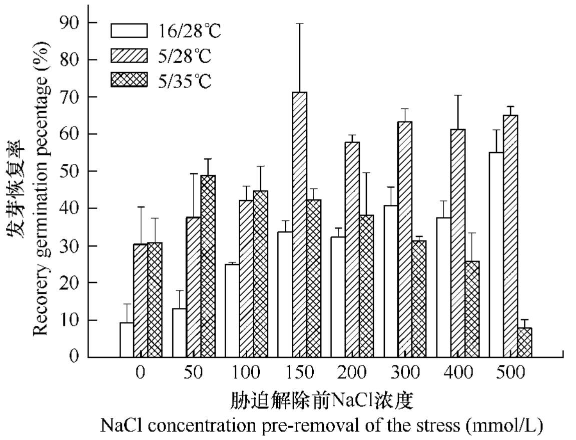


图4 胁迫解除前 NaCl 浓度和温度对羊草种子发芽率的影响

Fig. 4 Effects of pre-treatment salinity and temperature on the seed germination of *L. chinensis*

盐分与温度互作对植物种子萌发的抑制作用因物种不同而异[18,21,33~36],主要包括以下 4 种类型:(1)抑制作用在高温下更严重,如 *Sagittaria latifolia*[37];(2)在低温下更严重,如 *Halopyrum mucronatum*[18];(3)在高温和低温下抑制均非常严重,如 *Sporobolus ioclados*[21];(4)种子萌发的耐盐性与温度无关,如 *Arthrocnemum indicum*[38]。本实验中,温度和盐分互作对羊草种子的发芽率具有极显著的影响($p < 0.001$),说明其萌发对盐分的响应依赖于温度的变化,抑制作用表现为:16/28℃ >5/28℃,5/35℃ >5/28℃,表明羊草种子可能属于第 1 种类型,即抑制作用在高温下更严

重。根据种子萌发的耐盐度标准可以看出,羊草种子的耐盐适宜范围(发芽率为对照的 75%)、半致死浓度(发芽率为对照的 50%)、极限浓度(发芽率为对照的 10%)以及致死浓度(种子萌发完全被抑制)均以 5/28℃最高,其次是 16/28℃,在 5/35℃下耐盐性最差。

表 2　原盐浓度、温度及其互作对羊草种子发芽率和幼苗生长的影响

Table 2　Effects of salinity pre-removal of the stress, temperature and their interaction on germination and seedling growth of *L. chinensis*

| 变异来源 Source of variation | 发芽率 Germination percentage | 根长 Root length | 苗长 Shoot length |
|---|---|---|---|
| 盐分 Salinity | 3.9 | 7.2 | 72.7 |
| 温度 Temperature | 24.1 | 83.8 | 14.0 |
| 盐分×温度 Salinity×Temperature | 4.2 | 8.1 | 10.5 |

表中数据为双因素分析的 $F$ 值,显著水平均为 $p<0.01$. Data are $F$ values (Two-way ANOVA) significant at $p<0.01$

表 3　不同温度下羊草种子耐盐度

Table 3　Threshold values of salinity tolerance of *L. chinensis* under different temperature regimes

| 温度(℃) Temperature | 耐盐度 Salinity tolerance (NaCl mmol/L) | | | |
|---|---|---|---|---|
| | 耐盐适宜范围 Suitable concentration | 半致死浓度 Median lethal concentration | 极限浓度 Threshold concentration | 完全致死浓度 Total lethal concentration |
| 16/28 | <45 | 45 | 214 | 295 |
| 5/28 | 58 | 127 | 291 | 375 |
| 5/35 | <45 | <50 | 132 | 184 |

表中不同耐盐度数据是根据图 2 的回归方程计算得到　Data in the table were calculated from the regression functions in Fig. 2

不同物种的种子在解除盐胁迫处理后发芽恢复率不同[39],这种差异是由于种子萌发所需的温度梯度不同引起[40]。Gulzar 和 Khan[40] 研究表明,*Aeluropus lagopoides* 经 500 mmol/L NaCl 处理 20 d,在解除胁迫后,20/30℃变温条件下,发芽恢复率达到约 85%,而在 10/20℃下仅有 29%。在本研究中,羊草种子在经过 500 mmol/L 处理 18 d 后的,发芽恢复率在 5/28℃下最高达到 65.3%,其次是 16/28℃为 55.3%,在 5/35℃最低为 8.0%(图 4)。Huang 等[13]研究表明,盐处理 9 d 后,将 *Haloxylon ammodendron* 种子转移到蒸馏水中,盐分越高(800～1400 mmol/L),发芽恢复率越大(40%),低盐 50～600 mmol/L 仅提高 20%。高盐使得羊草种子进入强迫性休眠状态来阻止其萌发,随着雨季的到来,土壤表面盐分含量降低,外界环境如温度、水分等条件适宜的情况下才开始萌发,是羊草种子适应盐碱等生态环境的一种特性[25,41]。

盐对植物生长的抑制主要表现在渗透胁迫(引起水分的缺乏)、离子毒害和离子吸收的不平衡[42,43]。本研究表明,NaCl 胁迫均显著抑制了羊草的根长和苗长,且对苗长的抑制大于根长,这与 Ramoliya 和 Pandey[44] 的研究结论一致。随着 NaCl 浓度的增加,羊草幼苗的根/冠比呈上升趋势,表明盐对地下部分的抑制较小,而对地上部分生长影响较大,这可能是羊草适应盐碱环境

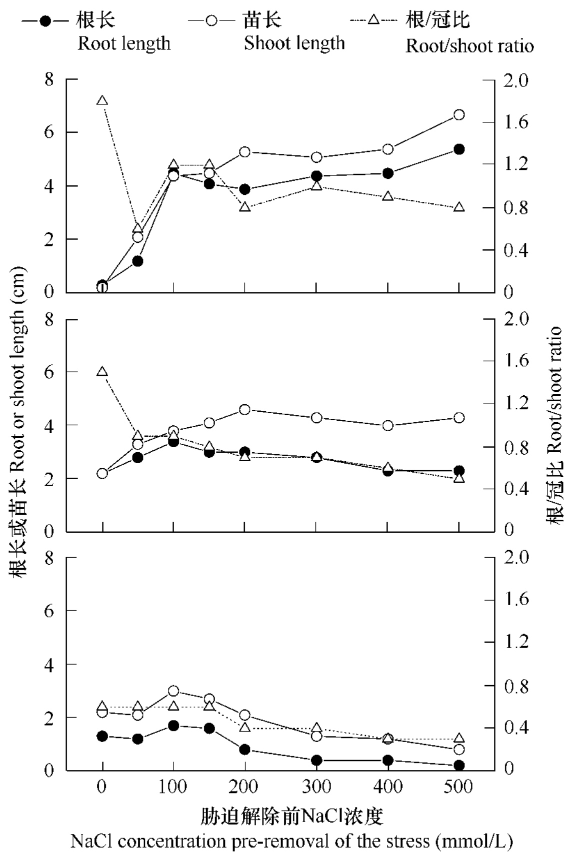


图 5　胁迫解除前 NaCl 浓度和温度对羊草幼苗生长的影响

Fig. 5　Effects of pre-treatment salinity and temperature on the seedling growth of *L. chinensis*

的一个主要原因。根/冠比是在环境因素作用下,经过植物体内许多基因变化过程和自我适应自我调节后最终表现出的综合指标。温度也显著影响羊草幼苗的生长,表现为温度过高和过低均不利于其生长。在相同低温(5/28℃和5/35℃)条件下,表现为5/28℃下较为适宜;在相同高温(5/28℃和16/28℃)条件下,则表现为16/28℃生长最佳,温度过高或过低均抑制了其生长。

本研究表明,羊草种子萌发期的耐盐能力差,当NaCl浓度超过50 mmol/L时发芽率被显著抑制。如何避开或降低羊草种子萌发和幼苗期的盐碱危害,是解决羊草生存和繁衍的关键问题之一。目前有以下3种途径:(1)通过育苗移栽恢复技术代替传统直播①,(2)培育耐盐碱新品种,(3)选择播种时间提高羊草种子萌发期的耐盐性。可以选择在雨季后播种,此时地表盐分经雨水淋洗含量减少,有利于提高盐碱条件下羊草种子发芽率。目前有关研究报道较少,在生产实践中能够应用的则更少,因此今后需加强本领域的研究,从而为盐碱化羊草草地的人工恢复提供技术支撑。

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